

Alaska Department of Fish and Game
Division of Wildlife Conservation
December 2000

Factors Limiting Moose at High Densities in Unit 20A

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**Federal Aid in Wildlife Restoration
Annual Performance Report
1 July 1999–30 June 2000
Grant W-27-3, Study 1.51**

This is a progress report on continuing research. Information may be refined at a later date.

If using information from this report, please credit the author(s) and the Alaska Department of Fish and Game. The reference may include the following: Boertje, R.D., C.T. Seaton, D.D. Young, M.A. Keech, B.W. Dale. 2000. Factors limiting moose at high densities in Unit 20A. Alaska Department of Fish and Game. Federal aid in wildlife restoration research performance report, July 1999-June 2000. Grant W-27-3, study 1.51. Juneau, Alaska. 43 pp.

RESEARCH PERFORMANCE REPORT

STATE: Alaska **STUDY:** 1.51

COOPERATOR: University of Alaska Fairbanks

GRANT: W-27-3

TITLE: Factors Limiting Moose at High Densities in Unit 20A

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PERIOD: 1 July 1999–30 June 2000

SUMMARY

We are monitoring moose (*Alces alces gigas*) reproduction, mortality, nutritional status, population size, trend, and composition in central Unit 20A. Central Unit 20A contains about 50% of the moose habitat and 67% of the moose in Unit 20A or about 1.1 moose/km² in a 6730-km² area in 1999. This is one of the highest moose densities for any equivalent-sized area in North America.

Our goal is to provide timely management recommendations aimed at keeping this high-density moose population from declining to low densities. Several authors have presented data indicating high-density continental moose populations should not be allowed to decline to low densities (Gasaway et al. 1983, 1992; Ballard and Larsen 1987; Bergerud and Snider 1988; Messier 1994; Van Ballenberge and Ballard 1994). These authors' conclusions were based on the predominance of data showing that combined wolf (*Canis lupus*) and bear (*Ursus arctos* and *Ursus americanus*) predation can keep moose populations at low densities (0.04–0.4 moose/km² in areas >2000 km²) for prolonged periods in Alaska, when human influence on wolves and bears is minimal. These low moose densities were described as well below food-limited densities and densities in which allowable harvests by humans were relatively low (Gasaway et al. 1992). Unit 20A differs in that human influence on predators has been moderate to high since 1976.

We hope to eventually maintain moose at moderate to high densities without repeating the Alaska Department of Fish and Game (ADF&G) wolf control program that apparently helped moose increase to high densities in Unit 20A (Gasaway et al. 1983; Boertje et al. 1996). Moose steadily increased from 1976 though 1991, beginning with the initiation of ADF&G wolf control (1976–1982). Since 1991, population estimates indicate the population has been relatively stable, although yearling recruitment declined during the deep snowfall winters of 1989–1990 through 1992–1993.

Our management recommendations during this reporting period included improving habitat, particularly in the Tanana Flats, and carefully monitoring and managing harvest of female moose. Habitat improvement is prudent because the nutrient regime of Tanana Flats moose is the lowest measured among continental wild moose populations. Careful harvest of females is practical because the early 1970s harvests of female moose were untimely and contributed to a major decline in the Unit 20A moose population (Gasaway et al. 1983). We recommended cessation of cow moose harvests in autumn 1999 because calf, yearling, and adult survival and twinning rates declined from May 1998 through May 1999. Current modeling indicates the population declined 10% between May 1998 and May 1999. However, no significant decline was evident from surveys of population size, and moose survival improved in 1999–2000, so we recommended resumption of minimal cow moose harvests in autumn 2000.

This report summarizes data collected from central Unit 20A from 1 March 1996–1 September 2000 when early winter moose density was high and stable and snowfall was at low to moderate levels. Fieldwork included initially collaring 44 adult female moose in March 1996. We subsequently spent 2 calving seasons (1996 and 1997) collaring newborn moose to evaluate causes and rates of calf mortality and 4 springs (March 1997–2000) collaring primarily 10-month-old moose with expandable adult collars. This is a unique study largely designed to evaluate cohort-specific reproduction and mortality. All samples of collared moose older than neonates were equally divided between the Alaska Range foothills and Tanana Flats. Virtually all moose calve in the Tanana Flats, and some subsequently move to the foothills. We evaluated nutritional status of the moose population by measuring parturition and twinning rates of adults, age of first reproduction, timing and synchrony of calving, weights of newborns and short yearlings, and, through ultrasonography, rumpfat depths of moose.

During this reporting period, we completed fieldwork on browse use and availability as part of a graduate student project conducted by CT Seaton. These quantitative browse studies will: 1) provide a baseline of browse information for comparisons with other areas, 2) potentially help describe why yearling moose residing in the Tanana Flats consistently weigh less than those migrating to the foothills, and 3) assist in prioritizing habitat management activities. Common browse species over much of Unit 20A are severely deformed by repeated heavy browsing or have grown beyond the reach of the moose, greatly reducing availability of winter forage.

Our observations support the hypotheses that Unit 20A moose exhibit low nutritional status yet high survival relative to other continental wild moose populations, as predicted from the high moose density and relatively high moose:predator ratios. Our most notable observations follow:

- The Unit 20A moose population is an intensively studied, high-use resource numbering about 11,000–12,000 moose since 1991 based on the 4 most precise population estimates (early winter 1991, 1996, 1998, and 1999). Annual harvest rates have increased during this period from about 4% to 6% of the prehunt numbers. Low snowfall winters have occurred since spring 1993, with the exception of moderate snowfall in the Tanana Flats in winter 1999–2000. Calving was clearly delayed and prolonged following the moderate snowfall of winter 1999–2000.

- Delayed age of first reproduction indicates moose in Unit 20A are experiencing the poorest nutrient regime recorded for continental wild moose in North America. For example, no 22-month-old moose were pregnant ($n = 38$). This has previously been well documented in only 2 of 19 studied moose populations in North America, both of which had other signs of better overall reproduction. Only 38% of 36-month-old moose ($n = 50$) gave birth, and 63% of 48-month-old moose ($n = 35$) gave birth, indicating most reproduction is delayed more than a year, compared with most other studied North American moose populations. Also, no cows <60 months old gave birth to twins, and the twinning rate for cows ≥ 36 months old was only 9% ($n = 185$).
- A 3.2-fold increase in moose numbers and a minimum 20% decline in production has occurred since 1978 in Unit 20A. The advantages of increased moose numbers far outweigh the disadvantages of lowered production for both consumptive and nonconsumptive users. Yet we recommend that any enhanced productivity stimulated by local habitat improvement projects go toward increasing harvest rather than further substantially increasing population size. The present density of moose is already one of the highest in North America; encouraging further increases in density will probably have a detrimental effect on the perpetuation of browse species and the long-term carrying capacity of the habitat.
- Poor nutrient regime is also indicated by dramatically lower short yearling weights in our study area ($\bar{x} = 163$ kg, $n = 111$), compared with short yearling weights in an adjacent moose population in Denali National Park ($\bar{x} = 207$ kg, $n = 8$), where nutrient regime is high (53% twinning rate). Short yearling weights in the Tanana Flats subpopulation were the lowest weighed in Alaska and were significantly lower every year compared to those we weighed in the Alaska Range foothills.
- We recommend collaring short yearlings with expandable collars to evaluate moose population condition. Age of first reproduction, twinning rates, and, particularly, short yearling bodyweights appeared to be sensitive relative indicators of nutrient regime among moose populations or subpopulations. Cohort-specific mortality rates were also valuable assets to modeling population trend. Costs to immobilize short yearlings were one-third those to immobilize adults. Flying transect surveys during calving was the preferred and least expensive method for evaluating twinning rates.
- Moose calves in Unit 20A experienced the highest survival rates (56% in the 1996 cohort and 52% in the 1997 cohort) documented among the 7 Alaska-Yukon moose calf telemetry study areas (19–42% survival in other areas). Also, survival was near 100% among moose 24 to 48 months old and averaged 86% annually for older moose.
- Wolves are the major predator on moose in Unit 20A, in contrast to other study areas in Alaska and the Yukon where black and grizzly bears are by far the primary predators. Wolves killed about 1850 moose annually in Unit 20A during the low to moderate snowfall years of 1996–1997 through 1999–2000 compared to about 790 harvested by humans, 730 killed by grizzly bears, 690 killed by black bears, and 390 that died from other causes.

- A stable population is predicted using average mortality and productivity data collected from May 1996 through May 2000, and a 2% decline is predicted using only data from May 1999 to May 2000.

Primary management goals are to sustain a high opportunity to harvest moose and to keep the moose density above levels in which combined wolf and bear predation can maintain moose at low densities. To responsibly manage this population at high densities, we need to know to what extent malnutrition, predation, and harvest affect population trend, particularly during adverse weather. This information is necessary, for example, to estimate sustainable yields of moose and optimum numbers of moose during various weather patterns. Maximizing harvest of female moose during favorable weather may be important to prolonging the period of high moose density. However, we believe that great caution must be exercised in harvesting moose in this system. Gasaway et al. (1983) concluded that mortality from severe winters, hunting, and wolf predation were largely additive in Unit 20A in the early 1970s and that underestimating the impact of harvest can lead to grave management problems.

Key words: Alaska, calving, harvest, management, moose, moose condition, mortality, predation, reproduction, rumpfat depth, survival, twinning.

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BACKGROUND

Moose (*Alces alces gigas*) in Unit 20A (Fig 1) are a unique, intensively studied, and highly valued resource (Gasaway et al. 1983; Boertje et al. 1996). Moose density in Unit 20A (0.85 moose/km² in a 13,044-km² area, Fig 2) is approximately 5–6 times higher than average moose densities in similar moose-wolf-bear systems in which wolves (*Canis lupus*) and bears (*Ursus arctos* and *Ursus americanus*) have been lightly harvested (Gasaway et al. 1992). High moose density in Unit 20A apparently resulted in part from Alaska Department of Fish and Game (ADF&G) wolf control during 1976–1982. Also, Unit 20A has had favorable weather

since 1975, except during 1989–1993, and much of Unit 20A has favorable moose habitat. Black and grizzly bear predation is low compared to wolf predation (Gasaway et al. 1983:30, this study). Grizzly bears and possibly black bears were reduced in a portion of our study area by local harvests during the mid to late 1980s (Hechtel 1991; Reynolds 1994). Also, during 1993 and 1994 ADF&G established a second wolf control program to increase caribou (*Rangifer tarandus*) numbers, and private trappers usually harvest 15–25% of the Unit 20A autumn wolf population each winter (Boertje et al. 1996).

Our study area in central Unit 20A (6730 km², Fig 1) contains about 50% of the moose habitat in Unit 20A and about 67% of the moose. For example, in 1996 we found 30% higher moose density in our study area compared to the total Unit 20A moose density. From this and historical distribution and habitat observations, we surmise that the study area encompasses some of the best moose habitat in Unit 20A.

No examples exist in either Alaska or the Yukon in which moose have maintained such a high density for long periods of time (>8 years) over a similarly large area (6730 km², Gasaway et al. 1992). We surmise from this that moose in our study area may eventually decline substantially from the combined effects of adverse weather, browse limitation, and uncontrolled wolf and bear predation (Gasaway et al. 1983, 1992). This was the case between 1965 and 1975 when the Unit 20A moose population declined from about 1.7 to 0.23 moose/km² (Gasaway et al. 1983). Aggressive fire suppression during the 1960s through the 1980s reduced the stimulation of browse production and nutrient cycling. Ill-timed harvest of cow moose also contributed to the magnitude of this decline.

Maintaining moose in Unit 20A above the level at which predation can strongly limit moose would be a significant wildlife management achievement. For example, elevated consumptive and nonconsumptive uses of moose would be ensured, hopefully without repeated intensive predator control programs. Gasaway et al. (1992) concluded that moose densities are predictably low (0.04–0.42 moose/1000 km²) where low harvest rates for wolves and bears prevailed for long periods in Alaska and the Yukon. Moose densities are higher in these same systems where humans significantly reduced predation or where wolves and bears are below food-limited levels for other reasons.

Since the mid-1970s, Unit 20A has proven to be Alaska's most intensively managed area in terms of ADF&G costs to survey wildlife and reduce predation for promoting increased moose and caribou numbers. This management focus has broad local support stemming primarily from a strong local tradition of hunting, awareness of the enhanced value of land with abundant wildlife, and gradual restrictions in hunting regulations elsewhere in Alaska. There is also widespread knowledge that Unit 20A moose densities and harvests were high during the 1960s, following federal predator control in the 1950s. Approximately 1500–3000 hunters have used Unit 20A annually since the late 1980s.

The 10-year decline of moose in Unit 20A, from about 22,000 in 1965 to about 2800 in 1975, taught us several important lessons (Gasaway et al. 1983). First, Unit 20A probably cannot sustain 1.5–1.9 moose/km² through adverse, deep snowfall winters when browse availability is reduced and energetic costs of obtaining browse are high. Second, wolves strongly impacted the declining moose population, as demonstrated by the wolf control program that

coincided with a sustained 15% finite annual increase in the moose population (Boertje et al. 1996). Third, errors were made in managing moose in the late 1960s and early 1970s. Biologists mistakenly believed that predators killed only moose that would soon die from other causes.

Today, biologists have proven techniques for estimating moose population size and trend (Gasaway et al. 1986), and radiotelemetry allows biologists to investigate causes and rates of moose mortality and changes in reproduction. Also, the potential effects of wolf and bear predation are better understood.

A current theory on wolf predation in wolf-bear-moose systems predicts that without periodic wolf control wolves will increase and combined wolf and bear predation will be sufficiently high to reduce the moose population to a low level (Sinclair 1989; Messier 1994; Hayes 1995). Under this theory, moose will soon return to low densities.

Under an alternative theory, wolves may restrict their own upper density and fail to reduce the moose population. For example, large wolf-territory size may restrict wolf density well below the level that wolves alone can reduce an elevated moose population to low densities. Moose may live at elevated densities for a protracted period under this theory.

The most plausible scenario is that high moose densities will continue until adverse weather intervenes; at this time browse limitation and predation may exacerbate the decline to low levels. For example, a moose population living at an overly high density may suffer greater nutritional impacts from adverse weather (Peterson and Page 1983; Messier 1995) and could potentially be accelerated to low levels by intense predation, even when moose:wolf ratios are initially relatively high (Gasaway et al. 1983). Predation can accelerate declines, particularly during and following severe winters, because of increased vulnerability of prey and underutilization of carcasses (Peterson and Page 1983). Overly high moose densities vulnerable to browse limitation are, therefore, cause for concern among managers, especially if the public requests that managers repeatedly control predation.

To examine these potential scenarios, we are studying the reproductive and nutritional vigor of an elevated moose population, weather variables, and the causes and rates of moose mortality in an area where humans do not annually control predation (Boertje et al. 1988; Gasaway et al. 1992:Fig 9). Parameters previously correlated with moose nutritional condition include yearling and adult pregnancy rates, adult rumpfat depths, adult twinning rates, and timing of calving (Boer 1992; Gasaway et al. 1992; Schwartz 1992; Stephenson et al. 1998). We focused our research on calf and yearling survival, short yearling weights, and age of first reproduction because young age classes are most sensitive to limiting factors such as predation, adverse weather, or food limitation. Companion projects will study dynamics of associated wolf, caribou, and grizzly bear populations.

Our goal was to determine what factors combine to influence the moose population and what management strategies are prudent to keep moose from returning to low densities. Current management options include 1) reducing harvest during autumns following reduced survival, and to reduce food limitation, 2) increasing harvest and 3) improving habitat. ADF&G is continuing efforts to burn portions of the Tanana Flats, either using wildfire or prescribed

burns. Suppression of wildfires has been common in Unit 20A, which reduces browse production and nutrient cycling.

OBJECTIVES

- Review literature on 1) moose biology and ecology at high densities; 2) indices to nutritional status of ungulates; 3) models of ungulate population dynamics; 4) predator-prey ratios in relation to population dynamics of moose, caribou, sheep (*Ovis dalli*), wolves, and grizzly bears; 5) predator/prey relationships in multiprey, multi-predator systems; and 6) population and harvest data on moose, caribou, sheep, wolves, and bears in Unit 20A.
- Estimate and evaluate the usefulness of several reproductive and condition indices for moose in Unit 20A.
- Determine causes and respective rates of mortality among radiocollared moose of various age classes in Unit 20A.

Graduate student Mark Keech tested the hypotheses that a relationship exists between dam condition and mortality of calves and that a relationship exists between neonatal variables of condition and mortality of calves. Several papers were published as part of this Masters degree program (Appendices A, B, and C). A second graduate student, CT Seaton, is documenting rangewide estimates of browse use and availability in the central Tanana Flats and Alaska Range foothills to provide baseline quantitative browse data for this malnourished moose population.

STUDY AREA

This study is being conducted in the central portion of Unit 20A (6730 km², Fig 1) where moose densities are highest. This area is bounded to the north by the Tanana River, to the west by Tatlanika Creek, to the south by the crest of the Alaska Range, and to the east by the Little Delta River. Unit 20A has been described by Gasaway et al. (1983), Boertje et al. (1996), and Keech et al. (2000).

METHODS

ADULT CAPTURE, CONDITION INDICES, RADIOTELEMETRY, AND MORTALITY

During 1–4 March 1996, we immobilized 22 adult female moose (>33 months old) in the Tanana Flats and 22 adult female moose and 1 yearling female in the Alaska Range foothills. During 10–13 March 1997 we recaptured 16 collared moose from the Tanana Flats and 12 collared moose from the Alaska Range foothills to reevaluate condition, and we captured 2 new adult female moose in the Tanana Flats. In March 1999 we radiocollared 4 new adult female moose in the Alaska Range foothills, and in March 2000 we radiocollared 7 new adult moose in the Alaska Range foothills, 9 in the Tanana Flats, and recaptured 2 34-month-old moose. We immobilized these moose with 3.0–4.5 mg (1.0–1.5 cc) carfentanil citrate (Wildnil[®], Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) and 150–167 mg (1.5–1.67 cc) xylazine hydrochloride (Anased[®], Lloyd Laboratories, Shenandoah, Iowa, USA),

administered intramuscularly via a 3 cc projectile syringe (2.9 cm needle) fired from an extra long range Palmer Cap-Chur[®] rifle (Douglasville, Georgia, USA). For reversal, we injected 300–450 mg (6–9 cc) of naltrexone hydrochloride (Trexonil[®], Wildlife Pharmaceuticals) and 350–400 mg (3.5–4.0 cc) tolazaline hydrochloride (Tolazine[®], Lloyd Laboratories) intramuscularly. Only 1 of 74 immobilized moose died and this moose was near death when darted. We used a Robinson R-44 helicopter for moose capture during 1997–2000 and 2 Robinson R-22 helicopters in 1996.

During 11–12 March 1998 we recaptured 22 22-month-old moose that were initially collared as 10-month-old moose, and during March 1999 we recaptured 13 22-month-old moose. No mortality was observed using the following drug doses: 2.7–3 mg (0.9–1.0 cc) carfentanil citrate and 100–110 mg (1.0–1.1 cc) xylazine hydrochloride delivered via a 2 cc projectile syringe (2.9 cm needle) and reversed with 275–300 mg (5.5–6 cc) naltrexone hydrochloride and 300–400 mg (3–4 cc) tolazaline hydrochloride given intramuscularly except for 2 cc given intravenously.

When moose were immobilized, we 1) measured neck girth of moose, hindfoot length, and total length along the dorsal body contour from the hairless patch on the nose to the tip of the tail bone; 2) measured depth of rump fat on the rump via ultrasound (Stephenson et al. 1998); 3) extracted a canine tooth as needed to determine age from cementum annuli (Matson's Laboratory, Milltown, Montana); and 4) collected 30–50 cc of blood from the jugular vein. R Zarnke (ADF&G, Fairbanks) processed blood samples. Serum was analyzed for antibodies (ADF&G, unpublished data) and pregnancy-specific protein B (PSPB, Bio Tracking, Moscow, Idaho USA). In 1996, serum was analyzed for 22 constituents (standard blood-serum profile, Fairbanks Memorial Hospital) and the acute phase protein haptoglobin (L Duffy, University of Alaska Fairbanks). T Stephenson (ADF&G, Soldotna, Alaska) diagnosed pregnancy status using transrectal ultrasonography in 1996 to compare to PSPB levels in blood samples (Stephenson et al. 1995).

We deployed Advanced Telemetry Systems (ATS, Isanti, Minnesota, USA) radio collars (model 9-2D-3V and 6V). Pulse rate of collars doubled when collars remained motionless for 5 hours (motion-sensing switch). We radiotracked adults daily in May and early June to detect newborn calves and listened to adult signals approximately monthly to monitor mortality rates. We used criteria and techniques described by Boertje and Gardner (2000) to evaluate causes of death.

SHORT YEARLING CAPTURE, CONDITION INDICES, RADIOTELEMETRY, AND MORTALITY

Our study design was unique in that we collared large numbers of short yearlings each year to study cohort-specific reproduction and mortality. We immobilized 17 short yearling female moose (10 months old) in the Tanana Flats and 17 in the Alaska Range foothills during 9–19 March 1997. During 3 and 9 June 1997, we immobilized 4 yearling female moose (12 months old) in the Tanana Flats with a lighter drug dose because 4 short yearlings died following capture in March. We immobilized short yearlings with 1.5 mg carfentanil citrate and 120 mg xylazine hydrochloride administered intramuscularly via a 2 cc projectile syringe (1.9 cm needle) fired from an extra long range Palmer Cap-Chur[®] rifle. We injected 150 mg of naltrexone hydrochloride intramuscularly to reverse the effects of the carfentanil citrate.

During March 1998, 1999, and 2000, we immobilized 20 short yearlings in the Tanana Flats and 20 in the Alaska Range foothills. No mortality was observed using the following drug doses: 1.2 mg (0.4 cc) carfentanil citrate and 60 mg (0.6 cc) xylazine hydrochloride delivered via a 1 cc projectile syringe and reversed with 125–150 mg (2.5–3 cc) naltrexone hydrochloride and 200–250 mg (2.0–2.5 cc) tolazoline hydrochloride given intramuscularly except for 1 cc given intravenously.

When moose were immobilized, we 1) measured neck girth and total length along the dorsal body contour from the hairless patch on the nose to the tip of the tail bone; 2) measured depth of rump fat via ultrasound (Stephenson et al. 1998); 3) weighed the moose with an electronic, calibrated strain gauge or dynamometer using an R-44 helicopter to lift the moose; and 4) collected 30–50 cc of blood from the jugular vein.

We deployed ATS radio collars (model 9-2D-6V). Extra overlapping collar belting and an attached bungee accommodated growth of yearlings. We experimented with recapturing these moose and detaching the bungee when moose were 22 or 34 months old and have found no problems with the collar design. Pulse rate of collars doubled when collars remained motionless for 5 hours (motion-sensing switch). We radiotracked yearlings approximately twice per month to monitor causes and rate of mortality (Boertje and Gardner 2000).

NEWBORN CALF CAPTURE, CONDITION INDICES, RADIOTELEMETRY, AND MORTALITY

We monitored pregnant collared females daily from fixed-wing aircraft (Piper PA-18 Super Cub) between 14 May and 13 June 1996 and 16 May and 9 June 1997. We noted births during early morning fixed-wing flights and captured calves in the afternoon. We captured 46 calves between 14 May and 3 June 1996, 28 from radiocollared cows and 18 from unmarked cows. In 1997 we captured 45 calves, 25 from radiocollared cows and 20 from unmarked cows between 16 May and 9 June. We distributed collars both geographically and temporally to mimic the calving of collared cows.

We captured newborns using a Jet Ranger 206 helicopter during 1996. During 1997 we captured most newborns using an R-44 helicopter. Cow-calf pairs were usually in clearings that permitted landing within a few meters of calves, and disturbance from the helicopter was usually sufficient to frighten dams away from the capture crew. If the cow-calf pair was not in or near clearings, the capture crew (with radio communication) exited the helicopter in the closest landing area. The helicopter then hovered above the calf in an attempt to frighten the dam away. We monitored all captures from fixed-wing aircraft. Some calves could not be captured without undue risk to the capture crew. If a calf of a radiocollared dam could not be captured, we captured a substitute calf from an uncollared dam in the same area. Capture success was most dependent upon the skills of the helicopter pilot. We released calves in less than 5 minutes (even if data collection was not complete) to minimize separation time. We used latex gloves and individual weighing and restraint bags (nylon bushel bags) to minimize transfer of scent. When twins were present, the crew captured and restrained both calves but processed only 1 and released both simultaneously.

We determined sex of calves and weighed calves by placing them in a bag and suspending them with a 25 kg Chatillon (Kew Gardens, New York, USA) spring scale. To estimate

birthweights, we subtracted 1.6 kg for each day >0.5 . This correction factor was based on regression models using weights of known-age calves. Due to uncertainty in estimating age beyond 4 days, birthweights obtained from calves estimated to be older than 4 days were omitted from statistical analyses involving birthweights. We also collected 3 cc of blood from the jugular vein. L Duffy (University of Alaska Fairbanks) analyzed serum samples for the acute phase protein haptoglobin during 1996.

During 1996 we deployed radio collars weighing 180 g each (ATS model 8C transmitters, 1.5 hr motion-sensing switch) constructed from 2 layers of 10 cm PEG[®] (Franklin Lakes, New Jersey, USA) elastic bandage (Osborne et al. 1991). During 1997 we deployed radio collars (200 g) constructed from 4 layers of elastic bandage. The day following capture we visually radiolocated calves to assure the pair had rebonded. Following visual confirmation of rebonding, we listened to calf signals to determine survival; flights were daily until 13 June and every other day until 30 June, after which the tracking interval gradually increased. Using a helicopter, we immediately investigated mortality signals. We used criteria and techniques described by Adams et al. (1995) and Boertje and Gardner (2000) to evaluate causes of death.

Eleven calves slipped collars from the 1996 cohort, 8 from collared dams and 3 from uncollared dams. We immediately censored calves of uncollared dams but visually located collared dams to evaluate calf mortality rates. If the calf was not observed with the collared dam on 3 consecutive flights, we assumed the calf had died. No calves from the 1997 cohort slipped collars.

STATISTICAL ANALYSES

Student's 2-tailed *t*-tests for pooled variances were used to analyze tabular data unless otherwise specified. To identify potential relationships between 22 serum constituents (standard blood profile) and rumpfat depth, we used multiple regression models (α to enter and stay = 0.15). We used regression to evaluate whether relationships existed between calving date and rumpfat depth or between cow age and rumpfat depth. We estimated survival rates for moose using Kaplan-Meier staggered-entry design for telemetry studies (Pollock et al. 1989). We used logistic regression to model the influence of the independent variables of neonate condition (birthweight, birth date, sibling status, and sex) on the dependent variable calf survival. We also used logistic regression to model the influence of the independent variables of cow condition (cow age, maximum rumpfat depth, midpoint rumpfat depth, and dam collaring location) on the dependent variable calf survival (Adams et al. 1995). Survival was broken down into 5 time intervals (1–30, 1–60, 1–140, 1–240, and 1–365 days); α for entry and inclusion into the model was set at 0.10 and a stepwise procedure was used. All analyses were completed using the statistical program SAS (SAS Institute Inc., Cary, North Carolina, USA), except for Kaplan-Meier estimates, *t*-tests, and chi-square tests (Remington and Schork 1970).

RESULTS AND DISCUSSION

ADULT FEMALE AGE STRUCTURE

A histogram of the ages of radiocollared moose older than calves (Fig 3) indicates the study population was well represented by young and middle-aged females in 1996. Mean age was 6.8 years ($s\bar{x} = 0.5$, range = 2–13, $n = 45$) in 1996.

REPRODUCTIVE INDICES

Given the high density of our study population and data summarized by Gasaway et al. (1992:Table 5) and Boer (1992), we predicted adult parturition rates of about 76–84% or lower, twinning rates of 0–25%, and low yearling pregnancy rates as observed for moose populations near and above carrying capacity. Our observations agree with our predictions; we observed a parturition rate of 77% ($n = 189$) and a twinning rate of 9% ($n = 185$) for moose ≥ 3 years old (Tables 1 and 2). Strong age-specific indicators of nutritional stress were even more noteworthy: 1) no 24-month-old moose ($n = 38$) were pregnant, 2) only 38% of 50 36-month-old moose and 63% of 35 48-month-old moose were parturient, 3) 3 (11%) of 29 cows appeared to delay giving birth until 60-months-old, and 4) no moose less than 60 months old produced twins (Tables 1 and 3). The reduced parturition rates in the 3- and 4-year-old cohorts made estimating productivity for the population problematic. For example, the estimated 77% parturition rate for moose ≥ 3 years old is inflated because 3- and 4-year-old moose were underrepresented in the sample of radioed moose most years, compared to the age structure of the population (Table 3, Fig 3).

These parameters indicate moose in Unit 20A are experiencing the poorest nutrient regime recorded for continental wild moose in North America (Schwartz 1998). The lack of yearling pregnancies has been well documented in only 2 of 19 other moose studies, and adult twinning rates were approximately twice as high in these 2 studies as reported here (Edwards and Ritcey 1958; Testa 2000).

We documented a minimum 20% decline in production with a 3.2-fold increase in density since 1978. Gasaway et al. (1983) estimated birth rates of 116 calves/100 cows ≥ 4 years old in 1977–1978 compared to our observations of 95 calves/100 cows ≥ 5 years old in this study (Table 1 and 3). This decline in reproduction reduces the sustainable harvest rate (Testa and Adams 1998). However, the substantial increase in moose numbers has allowed far greater sustainable yields than would have been possible at the lower density. The advantages of higher moose numbers far outweigh the disadvantages for both consumptive and nonconsumptive users. Yet we recommend that any enhanced productivity stimulated by local habitat improvement projects go toward increasing harvest rather than substantially increasing population size. The present density of moose is already one of the highest in North America; encouraging further increases in density will probably have a detrimental effect on the perpetuation of browse species and the long-term carrying capacity of the habitat. We hope to further analyze age-specific and density-dependent relationships in the productivity data by contrasting current data with data from the late 1970s (Gasaway et al. 1983).

We also expect to test whether raising a calf significantly reduces the chance of a subsequent pregnancy at current high densities because pregnancy rates derived from PSPB values

indicated a high annual variation, 98% ($n = 43$) in 1996 and 77% ($n = 30$) in 1997 for the same moose.

Transrectal ultrasonography and PSPB analyses produced identical results in 1996, the only year in which both results are available. Stephenson et al. (1995) also reported identical results using these methods. However, daily observations during the calving seasons indicate lower actual productivity in the population and less variability than indicated using ultrasound or PSPB. We use observed parturition rates as the best indicators of production in the population because they are most meaningful to the population and because of the likelihood of perinatal or intrauterine mortality in this high-density population. Indeed, each year for which data are available, daily observations failed to detect births among several cows that were confirmed pregnant through PSPB analyses. Inaccurate diagnoses occur when the embryo is dead or dies prior to birth.

Management staff have flown spring twinning rate transect surveys in central portions of the Tanana Flats for several decades without the use of radioed moose. Because these surveys more readily sampled moose from all age classes each year, these surveys more accurately estimated twinning rates in the population compared with our sampling of radioed moose (Table 2). Sampling must not bias against 3- and 4-year-old moose because these cohorts do not produce twins in the study area (Table 3). Undersampling of these 2 cohorts can lead to an overestimate of the population's twinning rate. For example, the radioed sample of moose twinned at a significantly higher rate than observed on transect surveys ($P = 0.023$, chi-square test of proportions, 2×2 table), presumably in part because 4-year-old moose were underrepresented in the radioed sample most years and because 3-year-olds were excluded in the sample (Fig 3, Table 2).

To further investigate the accuracy of twinning rate transect surveys, we tested whether differences in twinning rates could be observed with a helicopter (Bell 206) versus a fixed-wing aircraft (Bellanca Scout) and found no significant differences. Among 84 cows observed during the paired survey, 6 sets of twins were observed from the airplane (15% twinning rate, $n = 41$) and 7 from the helicopter (16% twinning rate, $n = 45$). Thus, paired airplane-helicopter surveys indicated no significant sightability handicap from the airplane (McNay 1990).

Preliminary data indicated that adult moose captured in the Tanana Flats were possibly experiencing less favorable environmental factors compared with moose in the Alaska Range foothills, but subsequent data do not support this hypothesis. Field observations from combined years 1996–2000 indicate moose captured in the Tanana Flats and Alaska Range foothills have similar productivity (Table 4, $P = 0.21$, chi-square test of proportions, 2×2 table).

SHORT YEARLING WEIGHTS

Moose are clearly exhibiting signs of nutritional stress from high density in Unit 20A. Short yearlings weighed in the study area in March averaged only 163 kg ($n = 151$) versus 207 kg ($n = 8$) in a low-density moose population in adjacent Denali National Park where the in utero twinning rate (60%) indicated superb nutritional status during ovulation (Adams 1999;

Stephenson et al. 1999). In addition, Adams weighed 12 6-month-old moose that averaged 195.7 kg in November 1998.

Weighing short yearling moose appears to be a particularly useful and relatively inexpensive tool for evaluating moose population condition. For example, we noted substantial differences between weights in the adjacent Denali and Unit 20A populations above. We also noted significant differences in weights between subpopulations within the study area. Short yearlings weighed in the Tanana Flats have weighed significantly less (about 17 kg less on average) than those in the Alaska Range foothills every year for 4 years ($P = 0.002\text{--}0.117$, t -test, Table 5). Although virtually all calves are born in the Tanana Flats, calves that move to the Alaska Range foothills in summer or autumn must have an improved energy balance relative to those remaining in the Tanana Flats.

Because of the reduced moose body weights in the Tanana Flats, we have assigned the Tanana Flats a higher priority for improving moose habitat compared to the Alaska Range foothills. Graduate intern and author CT Seaton is examining the timing of movements to the Alaska Range foothills and contrasting browse use and availability of moose in the Alaska Range foothills and the Tanana Flats.

NEWBORN CALF WEIGHTS

We expected birthweights to provide a relatively sensitive index to winter and spring maternal and range condition and that elevated birthweights would occur among the Alaska Range foothills subpopulation, in part because short yearlings weighed significantly more in the Alaska Range foothills. However, birthweights may provide only a nonsensitive index to winter and spring conditions. For example, we found no significant differences in newborn singleton or twin birthweights with regard to dam collaring location (Tanana Flats versus Alaska Range foothills, $P > 0.18$, paired t -test with pooled variances) or capture year ($P > 0.20$, t -test). Likewise, Ballard et al. (1996) found no increase in newborn calf weights following mild winter conditions.

Measuring moose birthweights is also problematic. Most investigators have failed to weigh newborns during radiocollaring operations. Indeed, Ballard et al. (1979) recommended against weighing newborns because of the increased likelihood of causing abandonment and because of the danger from dams when interfering with the cow-calf bond. The only comparative data from Interior Alaska are from the Yukon Flats.

As expected, newborn weights in Unit 20A are relatively low compared with those from the Yukon Flats, where moose density is 85% lower and the observed twinning rate (63%) indicates a high nutritional status during ovulation (Bertram and Vivion, in prep). Higher newborn weights in the Yukon Flats also indicate nutrient status of moose in spring is improved relative to Unit 20A. Singleton weights in Unit 20A (17.0 kg, $s = 2.6$, $n = 66$) were lower than those in the Yukon Flats (19.05 kg, $s = 1.7$, $n = 11$). Also, twins weighed 13.7 kg ($s = 1.6$, $n = 15$) in Unit 20A versus 16.81 kg ($s = 1.2$, $n = 30$) in the Yukon Flats. Twin calves weighed significantly less than singletons in Unit 20A ($P = 0.0001$, males and females pooled, t -test, Table 6). Schwartz and Hundertmark (1993) and Bertram and Vivion (in prep) also concluded that twins weighed significantly less at birth than singleton moose.

Our unique finding of a significant difference in birthweights between singleton male and female moose calves (Keech et al. 2000, Table 6, $P = 0.014$) may be an indication of the relatively poor nutritional status of moose in Unit 20A. Significant differences in weights of singleton male and female calves were not documented in other studies in which moose were in better condition (Schwartz and Hundertmark 1993, $P = 0.589$; Bertram and Vivion, in prep, $P > 0.5$). Indeed, Bertram and Vivion (in prep) observed that female newborns were heavier on average than males.

RUMPFAT DEPTHS

Depth of rump fat is an index to the condition of individual moose, and potentially an index to relative condition of a moose population. We initially hoped to contrast annual differences in rumpfat depths among young moose, e.g., moose in the 10- and 22-month-old cohorts, to provide a tool to evaluate annual differences in moose condition. We reasoned that young cohorts would have less variability in body condition than adult moose. However, we detected no rump fat among moose in these cohorts. This lack of rump fat apparently is a sign of malnutrition at the current high densities, given that some 22-month-old moose have fat in Denali National Park (L Adams, unpublished data). We examined 21 10-month-old moose and 20 22-month-old moose and detected no rump fat. Also, we detected no relationship between rumpfat depth and moose age for those individuals ≥ 34 months old (Fig 4), so we combined these data for further analyses.

Because short yearling bodyweights differed between the Tanana Flats and the foothills (Table 5), we expected to find significant differences in adult rumpfat depths from these 2 subpopulations. However, we found no significant differences ($P = 0.267$, t -test, Table 7). We conclude that adult rumpfat depths are less sensitive indices of nutrient regime compared to short yearling bodyweights, presumably because rumpfat depths were gathered from a sample of adults of all ages and reproductive histories. Perhaps with a greater sample size, rumpfat depths would detect significant differences in nutrient regimes in these subpopulations. However, costs for immobilizing adult moose are roughly 3 times that for immobilizing short yearlings, which makes weighing short yearlings a more attractive tool for evaluating moose population condition.

Low sample sizes in rumpfat depths also provided some confusing data when contrasting moose population condition between study areas. For example, rumpfat depths ($n = 10$) were equal in the Yukon Flats and Unit 20A (Stephenson et al. 1999; Bertram and Vivion, in prep). However, moose in the Yukon Flats were in better condition in spring (i.e., heavier newborn weights) and during ovulation in early winter (i.e., higher twinning rates [63%] compared with moose in Unit 20A. Also moose density in the Yukon Flats is about 85% lower than in Unit 20A and moose habitat is excellent (K Keilland, unpublished data). In contrast, rumpfat depths were about 2 times higher in Denali National Park where the moose density was also very low and the twinning rate was 60%.

We conclude that rumpfat depth is a more expensive and, at times, less sensitive index to nutrient regime in moose compared to twinning rates and weights of short yearlings. Several authors have previously described the utility of twinning rates in comparing nutrient regimes of moose populations (Boer 1992; Gasaway et al. 1992; Schwartz 1998). Twinning rates

provide a relatively inexpensive index to nutrient regime during ovulation in early winter. In contrast, short yearling bodyweights provide an index to nutrient regime in late winter.

We did find significant relationships between March rumpfat depths and reproductive status of females (Keech et al. 2000), but reproductive indices are much less expensive to collect than fat depths. Therefore, to evaluate relative moose population condition, we prefer monitoring reproductive indices (Boer 1992), rather than collecting expensive rumpfat data.

Mean maximum depth of rump fat was significantly greater ($P = 0.0002$, t -test) among pregnant versus nonpregnant adult cow moose (Table 8). Mean maximum depth of rump fat was also significantly greater for moose observed parturient versus those never observed with a calf ($P = 0.004$) and for dams giving birth to twins versus those with singletons ($P = 0.001$). We also found that the fattest dams produced on average the heaviest calves. Regression indicated birthweight of singleton neonate moose was positively ($P = 0.0003$, $R^2 = 0.29$) related to March rump fat of their dam (Fig 5).

BLOOD PARAMETERS OF CONDITION

The acute phase protein haptoglobin in serum samples may be helpful in distinguishing stressed from nonstressed mammals (Duffy et al. 1993; Zenteno-Savin et al. 1997). No detectable levels of haptoglobin were present in any of our calf ($n = 43$) or adult ($n = 44$) serum samples from 1996.

With the blood obtained from adult female moose in 1996, we attempted to identify potential relationships between 22 serum constituents (standard blood profile) and rumpfat depth using multiple regression models. A model using creatinine and AST met all the necessary criteria but accounted for only 33.7% (adjusted R^2) of the variability observed (Keech et al. 1998). We conclude, at this time, that standard serum constituents are not useful indicators of rumpfat reserves in moose.

CALVING DATES AND CORRELATIONS WITH DAM RUMP FAT

Reduced snow depths during winter 1995–1996 may have contributed to earlier calving in 1996 compared to subsequent years (Table 9). Also, delayed calving in May 2000 followed deep snowfall in the Tanana Flats (but not in the foothills). Only following adverse winters with deep snow has most of the calving in this area been delayed until June (prior ADF&G unpublished data). Extremes in the timing and synchrony of calving during this study are depicted in Figure 6.

If adverse winter weather delays calving or if poor autumn condition delays conception, we would predict that dams with the earliest births might have the greatest March fat reserves. As expected, regression indicated a significant ($P = 0.009$, $R^2 = 0.108$, $n = 62$) negative relationship (slope = -0.062) between julian calving date and maximum March rumpfat depth. Data are needed following more adverse winter weather to further study this relationship.

NATURAL MORTALITY AND HARVEST OF MOOSE OLDER THAN CALVES

Adult natural mortality varied from 7–21% annually during this study (Table 10). In contrast, almost no mortality was observed between the ages of 24 and 48 months. We are well positioned to evaluate mortality rates of 48- to 60-month-old moose this year. Gasaway et al. (1983:24) previously reported a lack of mortality among young adult age classes in this moose population during 1973–1978.

Yearling mortality rates averaged 13% during 1997–1998, increased to 33% during 1998–1999, and declined to 17% in 1999–2000 (Table 10). The increased mortality rate in 1998–1999 was probably not realized in the population but a function of the moose sampled. For example, snowfall during winter 1998–1999 was low and short yearling bodyweights in 1999 were higher than other years (Table 5). Also, November population surveys indicated 33 yearlings/100 cows \geq 28 months old in 1997, 20 in 1998, and 14 in 1999. Timing of mortality of yearlings ($n = 26$) indicates 54% of the annual mortality occurs from mid-May until the first of November.

Wolf predation was the major cause of death among adult and yearling moose. In 19 cases where we were able to investigate the cause of death of radioed adults, wolves killed 14 (74%), grizzly bears killed 2 (11%), and 3 (16%) died from factors other than predation. Of 26 yearlings (12–24 months old) that died, wolves killed 17 (65%), bears killed 7 (27%), and 2 (8%) died from other factors.

Hunters took a nominal harvest of cows in the study area during September 1996, 1997, and 1998. These were the first legal cow harvests since 1974. The department has issued 300 drawing permits annually with 65–75 cows reported harvested each year. The 1996–1999 reported bull harvests totaled 610–660 ($\bar{x} = 625$). The harvest rates totaled 6% of the prehunt population each year, if we multiply the reported bull harvest by 1.15 to account for unreported harvest and mortally wounded moose that were lost. Using similar methods to estimate total harvest, Boertje et al. (1996) documented a 4% average annual harvest rate in Unit 20A during the previous 20 years. We did not issue cow permits in Unit 20A during 1999 because of declining survival rates of calf, yearling, and adult moose and lower than expected estimates of population size (Table 10, Fig 2). We recommended resumption of cow hunts in 2000, and our recommendations were accepted. Also, following our recommendations, bull hunting seasons were shortened and some antler restrictions were added to certain hunts because of declining bull:cow ratios (23 bulls/100 cows in 1999).

CALF MORTALITY

The 1996 and 1997 radiocollared newborn calves experienced the highest annual survival rates (52–56%, Table 10) among the 7 Alaska-Yukon moose calf telemetry studies conducted to date. Previously reported annual calf survival rates were 19% (Larsen et al. 1989), 20% (Bertram and Vivion, in prep), 25% (Gasaway et al. 1992), 29% (Osborne et al. 1991), 32% (Ballard et al. 1991), and 42% (Franzmann et al. 1980) using similar techniques. High calf survival undoubtedly contributes to the reduced reproductive performance of this population (Testa and Adams 1998).

Unfortunately calf:cow ratios declined in Unit 20A in 1998 to the lowest observed since 1986 (Boertje et al. 1996). Calves per 100 cows ≥ 28 months old were 35.8 in 1999, 34.5 in 1998, 40.1 in 1997, and 47.3 in 1996. In part because of this decline in calf survival, we proposed to temporarily eliminate the 1999 cow harvests in Unit 20A.

In the final report we will compare the mortality rates of singleton calves among studies because twin calves experienced significantly lower survival rates compared with singletons ($P < 0.05$, log-rank test, Fig 7). Osborne et al. (1991) previously reported lower survival of twins. Protecting 2 calves from predators is probably more difficult than protecting a single calf (Stephenson and Van Ballenberghe 1995).

Predation was by far the major proximate cause of death in this and all previous moose calf mortality studies. Wolves killed more calves than both bear species in this study, while grizzly bears and black bears killed about equal proportions of calves (Fig 8, Table 11). In previous moose calf mortality studies, either black or grizzly bears were clearly the major predator.

In addition to mortality detected using radiocollared calves, mortality prior to birth or perinatal mortality during the first 24 hours after birth apparently occurred in 7 (17%) of 42 pregnancies in 1996 and 3 (13%) of 23 pregnancies in 1997. These were cases in which births were not detected during daily flights. Pregnancy was assumed based on transrectal ultrasonography and PSPB analyses in March 1996 and PSPB analyses in March 1997. Causes of these deaths are difficult to determine. Predation is only partly responsible for these deaths (Whitten et al. 1992; Boertje and Gardner 2000:14). For example, during helicopter flights, we observed 2 stillborn calves (1 each in 1996 and 1997), 1 from a set of twins and 1 apparently a singleton, both born to radiocollared cows.

We collared 91 newborn calves during 1996 and 1997 to estimate the mortality rate of calves we observed from fixed-wing flights. Eight calves died from capture-related incidents (abandonment or trampling by dam following release), and we censored these from the analysis. One transmitter failed within a few weeks of deployment and 1 failed a few months later.

RELATIONSHIP BETWEEN NEONATE CONDITION AND CALF MORTALITY

We studied the relationship between calf survival and birthweight, birth date, and sex for singleton calves from combined data for 1996 and 1997. No variables entered the logistic regression model for the survival interval 1–30 days. These data indicate that all calves are equally vulnerable to mortality factors common to this first month of life. However, for survival intervals age 1–60 and 1–140 days, birthweight entered the model ($P = 0.011$ and 0.007 , respectively), indicating increased mortality of lightweight calves (parameter estimates were -0.26 and -0.25 , respectively). Keech et al. (1999) documented that low birthweight calves remain among the smallest in their cohort. No variables entered the model for the interval 1–240 days. These data were analyzed further by Keech et al. (2000, Appendix C).

RELATIONSHIP BETWEEN ADULT CONDITION AND CALF MORTALITY

Preliminary analysis of the data supports the hypothesis that no relationship exists between dam condition (age, fat reserves, and collaring location) and mortality of their calves within the range of values observed. Neither dam age, fat reserves, nor dam collaring location entered the logistic regression model during any time interval. However, a weak indirect relationship between dam condition and calf survival may exist based on the observed relationship between dam rump fat and calf weight (Fig 5). More values are needed from more nutritionally stressed moose to further study this relationship. Data are discussed further by Keech et al. (2000, Appendix C).

POPULATION MODELING

To derive a conceptual model of moose population dynamics in Unit 20A, we averaged data on annual estimates of population size (Fig 2), productivity, and mortality factors for the 4 low to moderate snowfall years of 1996–1997 through 1999–2000 (Table 11). Methods were previously published by Gasaway et al. (1992, Appendix D) and Boertje and Gardner (2000). The moose population derived is stable and wolves are the primary predator killing about 13% of the postcalving population annually (Table 11). In contrast, humans, grizzly bears, and black bears each kill about 5% of the postcalving population annually. A 10% decline in the population is predicted using only data during 1998–1999, and a 2% decline is predicted using data from 1999–2000.

CONCLUSIONS

Moose in the study area are clearly nutritionally stressed. Bodyweights of short yearlings are extremely low, and the high density compromises reproduction in regard to delayed age of first reproduction and low twinning rates. ADF&G is actively pursuing prescribed burns in Unit 20A to increase abundance of available browse. Common browse species in much of Unit 20A are severely deformed by repeated heavy browsing or have grown beyond the reach of moose.

Continued telemetry studies of young cohorts are recommended to discern the effects of high density and severe weather on this unique, high-density moose population. We have data from only 3 mild winters and 1 moderate winter, and we expect to see much more variability in condition and survival following a winter of heavy snowfall.

Modeling exercises using data on productivity and mortality of the respective age classes indicate the population was probably slowly increasing during 1996–1998 and decreasing during 1998–2000, but population surveys indicate a nearly stable population since 1991. Wolves are the major predator, unlike previous studies of moose in Alaska and the Yukon.

A primary goal is to provide maximum sustained opportunity to harvest moose at moderate to high densities without repeating the previous wolf control programs. A priority is to keep the moose density from falling to densities in which predation strongly limits human uses of moose (Gasaway et al. 1983, 1992). We hope to determine an optimum range of moose numbers for Unit 20A. Ideally, we want to see moose at high numbers but not so high that the

long-term perpetuation of browse species is jeopardized and severe declines occur from the combined effects of initial adverse weather, high predation, and poor range condition.

ACKNOWLEDGMENTS

Study costs were supported by funds from Federal Aid in Wildlife Restoration, the state of Alaska, and the US Forest Service. We thank T Boudreau, L Butler, J Crouse, E Finch, L Fox, R Hunter, E Lenart, M McNay, T Osborne, J Selinger, T Stephenson, K Taylor and R Zarnke, all from ADF&G, who helped with various portions of field and laboratory work. M Webb ably piloted fixed-wing aircraft during radiotracking flights and J Larrivee and T Cambier were the most skilled helicopter pilots. We also thank RT Bowyer (Institute of Arctic Biology, University of Alaska Fairbanks), V Van Ballenberghe (US Forest Service, Pacific Northwest Research Station), JW Testa, P Valkenburg, J Ver Hoef, and T Stephenson (ADF&G) for their assistance and comments on data analysis and manuscript preparation.

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Figures

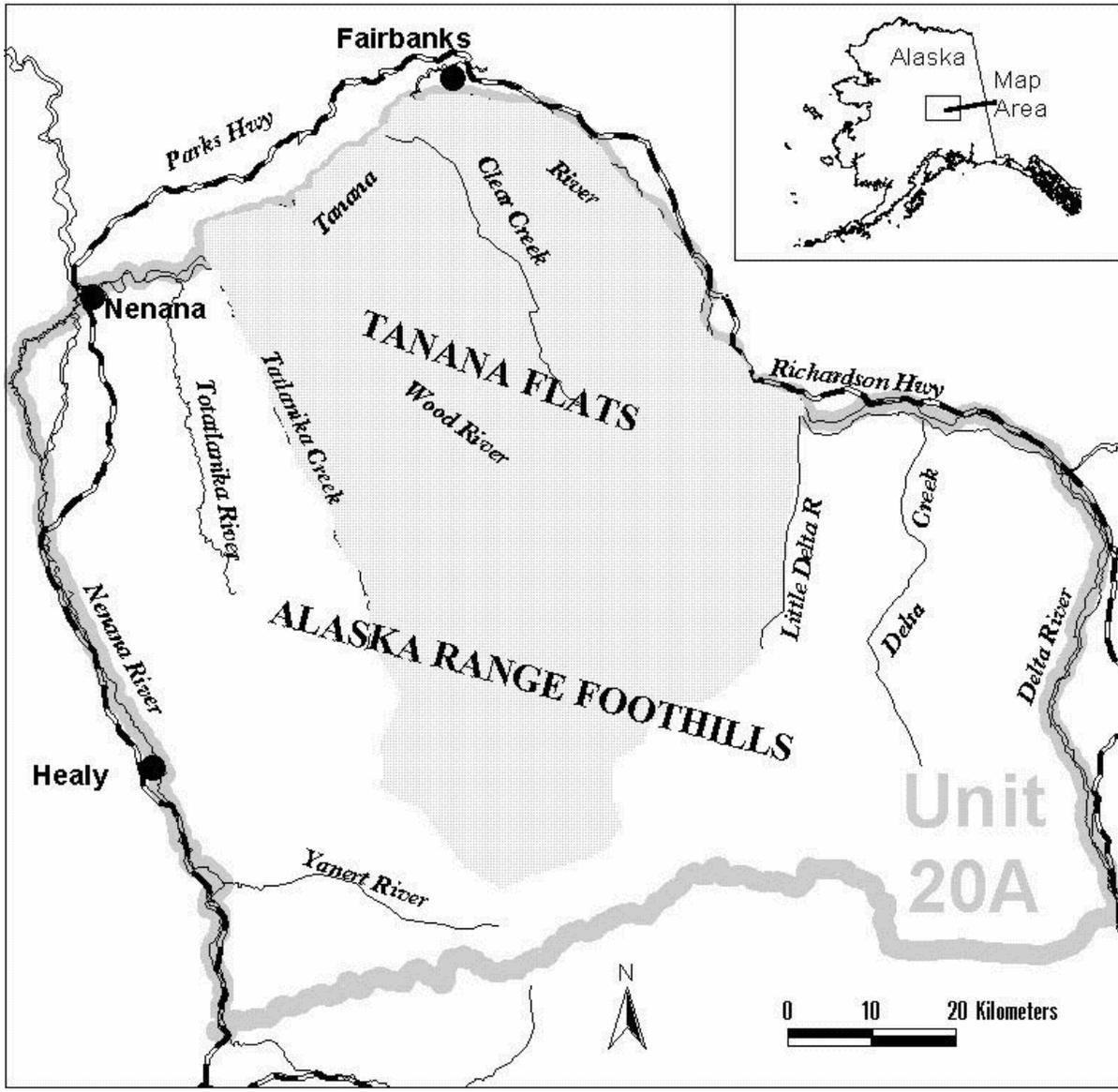


Figure 1 Shaded portion is the 6730-km² study area in central Unit 20A. About 67% of the moose in Unit 20A reside in the study area. Unit 20A contains about 13,044 km² of moose habitat.

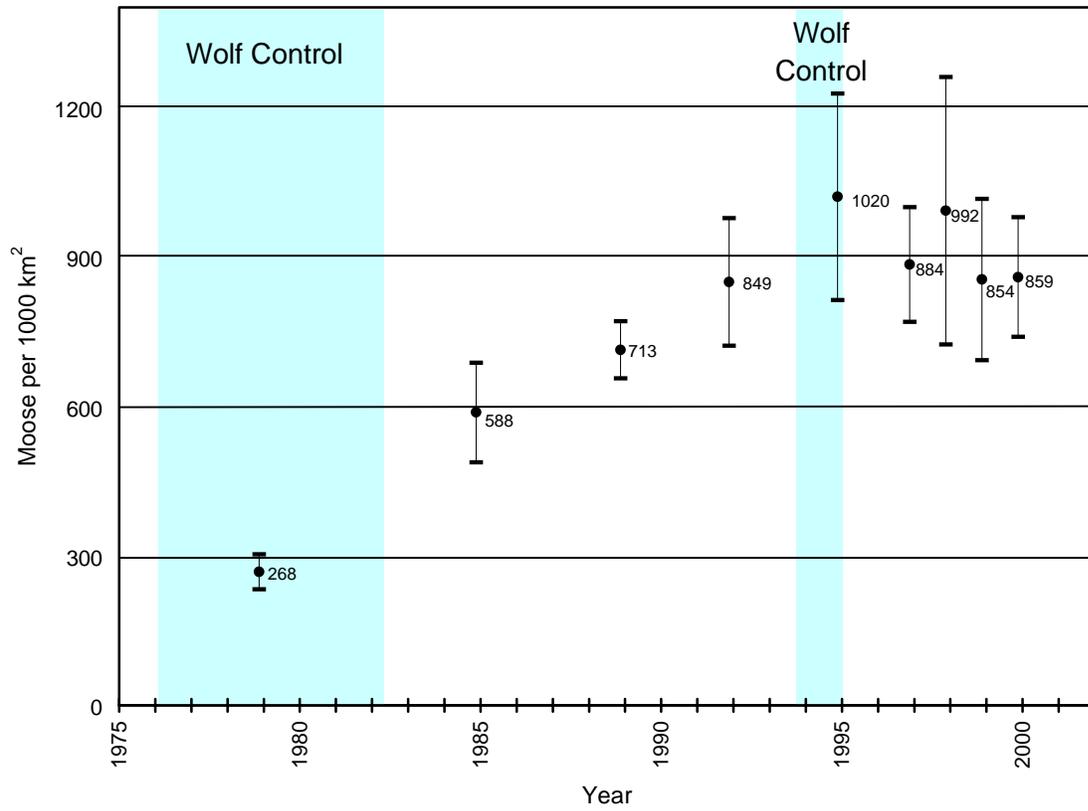


Figure 2 Moose density estimates (\pm 90% CI) in 13,044 km² of moose habitat in Unit 20A, Interior Alaska, 1978–1999. Data from 1978–1994 are described by Boertje et al. (1996). More recent estimates are from ADF&G files.

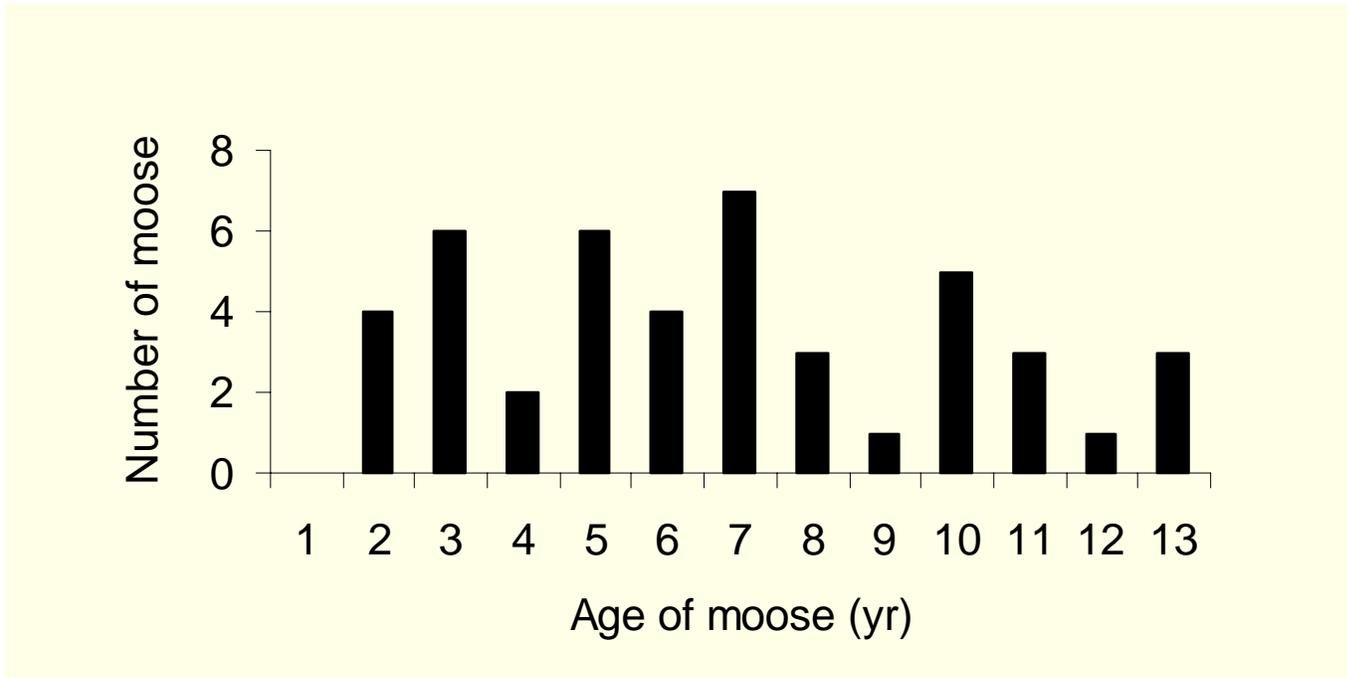


Figure 3 Age structure of 45 radiocollared moose ≥ 2 years old, central Unit 20A, March 1996. Data are from cementum annuli of canines (Matson's Laboratory, Milltown, Montana, USA).

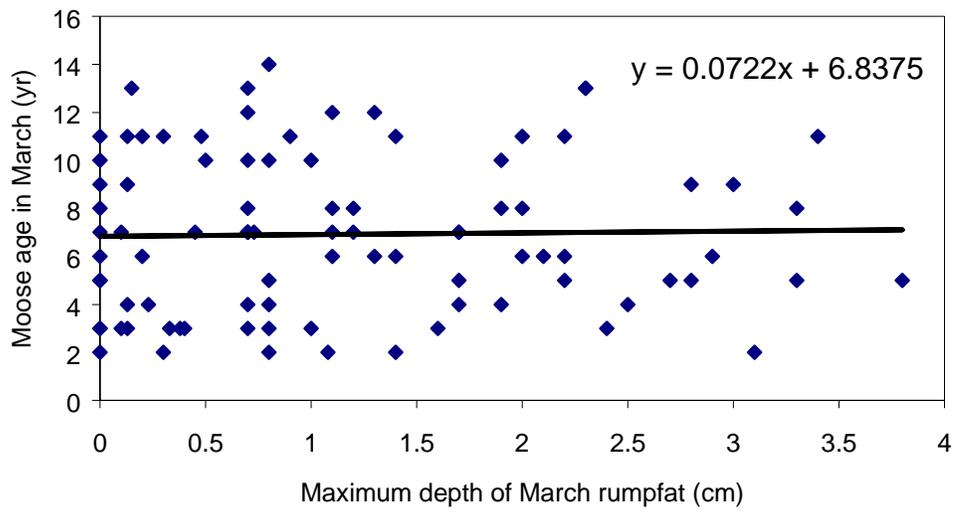


Figure 4 Relationship between adult female age in March and maximum depth of rump fat, central Unit 20A, 1996, 1997, and 2000 data combined, $P = 0.84$, $R^2 = 0.0005$, $df = 88$

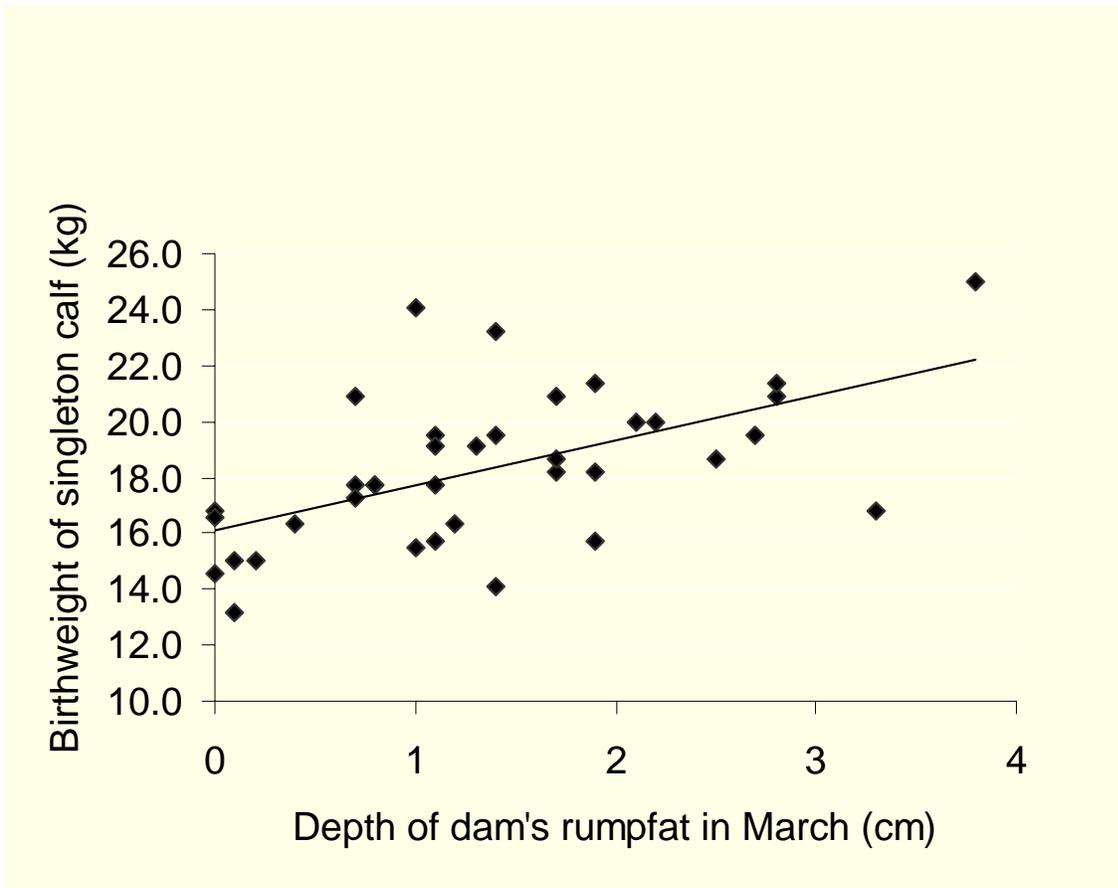


Figure 5 Relationship between singleton calf birthweight in May and depth of dam's rump fat in March, central Unit 20A, 1996 and 1997 data combined, $P = 0.0003$, slope = 1.60, $R^2 = 0.29$

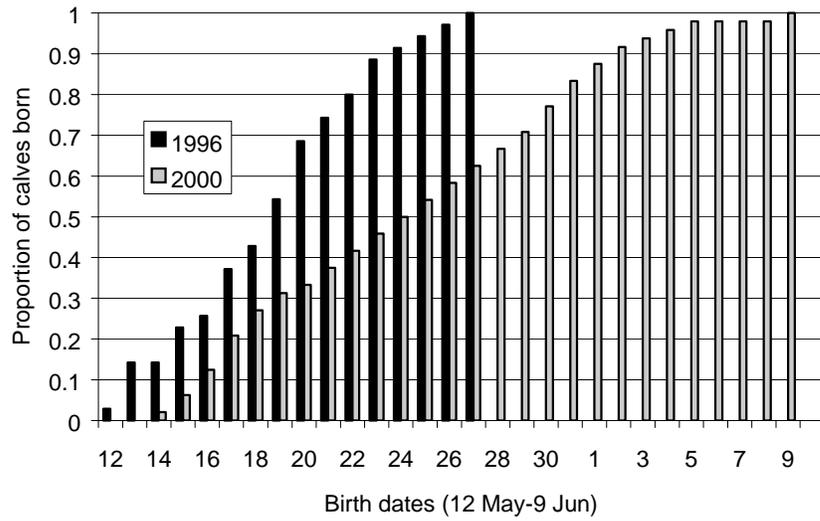


Figure 6 Cumulative proportion of radiocollared dams giving birth during the earliest calving season (1996) and the latest calving season (2000) during this study, central Unit 20A

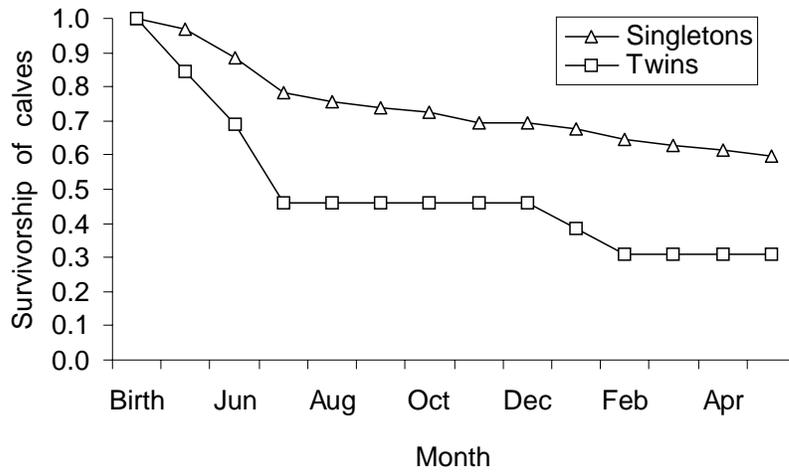


Figure 7 Survivorship of radiocollared singleton ($n = 70$) and twin ($n = 13$) moose calves born in the 1996 and 1997 cohorts, Unit 20A. Survivorship functions were significantly different ($P < 0.05$), log-rank test.

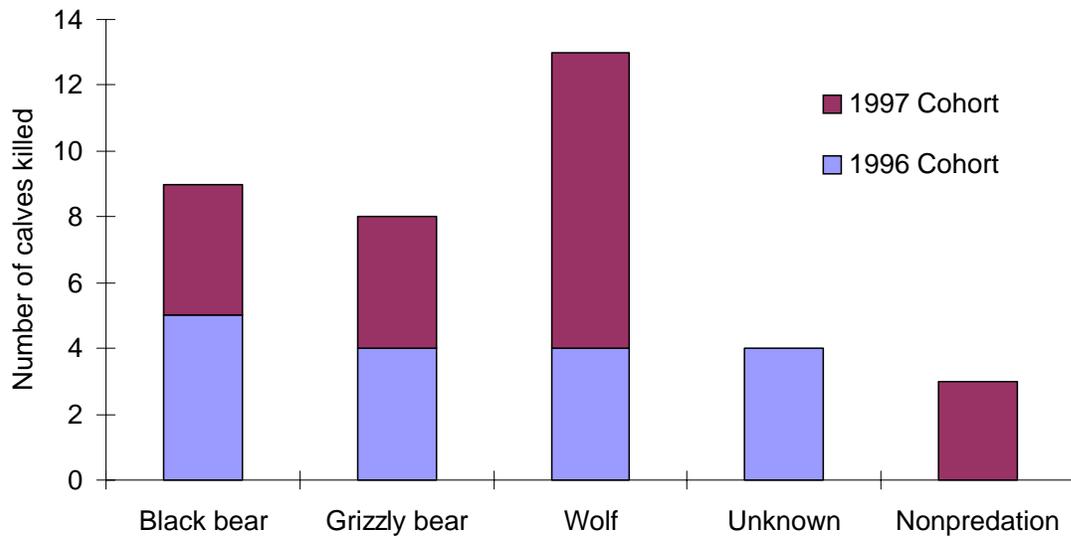


Figure 8 Causes of death among 37 radiocollared moose calves (aged 0 to 12 mo) that died in the 1996 and 1997 cohorts in central Unit 20A. Nonpredation mortality included 1 calf that died from drowning/exposure (Sep–Oct), 1 calf that died from malnutrition (Feb), and 1 calf that died from injuries inflicted by a moose during the rut.

Tables

Table 1 Observed proportions of parturient radioed moose, 1996–2000, central Unit 20A. Data on 24-month olds are from PSPB analyses of blood collected at 22 months of age. The remaining data are from daily observations of successful births in May and early June and negative PSPB results from blood collected the prior March. Positive PSPB results were considered inaccurate because daily observations could not confirm successful births. Ages were determined when moose were radioed as calves (March 1997–1999) or through cementum analysis of teeth when moose were older than calves.

Year	Proportion of radioed moose observed with newborn calves (%)						
	24 months old	36 months old	48 months old	5–9 years old ^a	10–16 years old ^b	All cows 5 years and older	Cows radioed at ≥36 months old ^c
1996	0/1	1/3	4/6	20/21 (95)	10/13 (77)	30/34 (88)	35/43 (81)
1997		0/2	1/3	17/22 (77)	11/14 (79)	28/36 (78)	29/41 (71)
1998	0/23		2/2	13/19 (68)	15/17 (88)	28/36 (78)	30/38 (79)
1999	0/13	10/22 (45)	1/1	11/14 (79)	11/14 (79)	22/28 (79)	23/29 (79)
2000	0/1	8/23 (35)	14/23 (61)	15/16 (94)	11/17 (65)	26/33 (79)	28/38 (74)
Total	0/38 (0)	19/50 (38)	22/35 (63)	76/92 (83)	58/75 (77)	134/167 (80)	145/189 (77)

^a The 5-year-old rate was 12/15 (80%) and the 9-year-old rate was 15/17 (88%).

^b The 10-year-old rate was 11/14 (79%).

^c These are inflated parturition rates for these age classes because 3- and 4-year-old moose are underrepresented in the sample of radioed moose in most years (Fig 3), e.g., $n = 3$ 3-year-olds in 1996, 2 in 1997, 0 in 1998, 0 in 1999, and 1 in 2000.

Table 2 Twinning rates among parturient radioed moose ≥ 4 years old in May compared with rates among parturient moose ≥ 3 years old observed on late May transect surveys, 1996–1999, central Unit 20A. No transect surveys were flown in 2000.

Year	Twining rates (%) among parturient moose in May			
	Daily observations of radioed moose ≥ 4 years old		Moose observed on transect surveys (≥ 3 years old)	
	%	<i>n</i>	%	<i>n</i>
1996	32	34	18	40 (26 May)
1997	10	29	12	26 (21 May)
1998	20	30	7	55 (26, 30 May)
1999	4	23	3	64 (25, 26 May)
Combined years	18 ^{a,b}	116	9 ^b	185

^a This is a maximum rate because 4-year-old moose did not give birth to twins during this study and are underrepresented in the sample of radioed moose in some years (Table 3, Fig 3).

^b Pooled twinning rates were significantly higher using observations of radioed moose versus observations of moose on transect surveys ($P = 0.023$, chi-square test, 2×2 table). We deem the transect surveys a more accurate measure of the population's twinning rate because the age structure of the sample is not biased, as is the case in the radioed sample (Table 3, Fig 3).

Table 3 Observed proportions of twin births among parturient radioed moose, 1996–2000, central Unit 20A. Data are from daily observations of successful births in May and early June. Ages were determined when moose were radioed as calves (March 1997–1999) or through cementum analysis of teeth when moose were older than calves.

Year	Proportion of twin births among radioed cows observed with calves (%)				
	36 months old	48 months old	5–9 years old	10–16 years old	All cows 5 years and older
1996	0/1	0/4	6/20 (30)	5/10 (50)	11/30 (37)
1997		0/1	3/17 (18)	0/11 (0)	3/28 (11)
1998		0/2	4/13 (31)	2/15 (13)	6/28 (21)
1999	0/10	0/1	0/11 (0)	1/11 (9)	1/22 (5)
2000	0/8	0/14	1/15 (7)	2/11 (18)	3/26 (12)
Total	0/19	0/22	14/76 (18)	10/58 (17)	24/134 (18)

Table 4 Observed parturition rates among radioed moose ≥ 4 years old in May in the Tanana Flats and adjacent Alaska Range foothills, May and June 1996–2000, central Unit 20A

Year	Observed parturition rates (%) of moose ≥ 4 years old in May					
	Tanana Flats		Alaska Range Foothills		Combined areas	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
1996	89	19	81	21	85	40
1997	55	20	95	19	74	39
1998	79	19	79	19	79	38
1999	80	15	79	14	79	29
2000	69	29	74	27	71	56
Combined years	74 ^a	102	81 ^a	100	77	202

^a Pooled parturition rates did not differ ($P = 0.206$, chi-square test, 2×2 table) between radioed moose in the Tanana Flats versus those in the Alaska Range foothills.

Table 5 Average weights of female short yearlings 10 months old in the Tanana Flats and adjacent Alaska Range foothills, March 1997–2000, central Unit 20A

Year	Weights of 10-month-old female short yearlings (kg)								
	Tanana Flats ^a			Alaska Range foothills ^a			Combined Areas		
	<i>x</i>	<i>s</i>	<i>n</i>	<i>x</i>	<i>s</i>	<i>n</i>	<i>x</i>	<i>s</i>	<i>n</i>
1997	154.2	25.0	17	164.5	24.7	17	159.2	25.0	34
1998	150.9	20.9	20	169.4	19.1	20	160.2	21.9	40
1999	158.9	17.7	18	178.0	18.9	19	168.7	20.5	37
2000	153.2	24.9	20	174.3	20.2	20	163.7	24.8	40
Combined years	154.2	22.1	75	171.7	20.9	76	163.0	23.1	151

^a Moose weights in the Tanana Flats were significantly less than those in the Alaska Range foothills ($P = 0.0001$, F value = 16.00, Type III sums of squares, SAS software). Weights in the flats were also significantly less using annual data; in 1997 $P = 0.117$, in 1998 $P = 0.003$, in 1999 $P = 0.002$, in 2000 $P = 0.003$ (one-tailed t -test with pooled variances).

Table 6 Average birthweights for singleton and twin newborn moose, 1996 and 1997, central Unit 20A

Year	Singleton birthweights (kg) ^a						Twin birthweights (kg) ^a					
	Males ^b			Females ^b			Males			Females		
	\bar{x}	<i>s</i>	<i>n</i>	\bar{x}	<i>s</i>	<i>n</i>	\bar{x}	<i>s</i>	<i>n</i>	\bar{x}	<i>s</i>	<i>n</i>
1996 ^c	18.4	3.0	9	16.4	2.6	17	14.1	2.4	4	13.5	1.4	6
1997 ^c	17.6	2.2	15	16.2	2.3	21				14.4	1.1	3
Combined (1996–1997)	17.9	2.5	24	16.3	2.4	38	14.1	2.4	4	13.8	1.3	9

^a Male singletons weighed significantly more than male twins in 1996 ($P = 0.0294$) and combined 1996–1997 ($P = 0.0092$). Female singletons weighed significantly more than female twins in 1996 ($P = 0.0174$) and combined 1996–1997 ($P = 0.0049$), *t*-test.

^b Male singletons weighed significantly more than female singletons in 1996 ($P = 0.0893$), 1997 ($P = 0.0779$), and combined 1996–1997 ($P = 0.0144$), *t*-test.

^c No significant difference between 1996 and 1997 birthweights ($P > 0.2$) within sex or sibling status, *t*-test.

Table 7 Average maximum rump fat depths of female moose ≥ 34 months old from the Tanana Flats and adjacent Alaska Range foothills, March 1996, 1997, and 2000, central Unit 20A. The 1996 moose were subsampled in 1997, therefore these are not independent samples.

Year	Adult maximum rumpfat depth (cm)								
	Tanana Flats			Alaska Range foothills			Combined		
	\bar{x}	$s_{\bar{x}}$	n	\bar{x}	$s_{\bar{x}}$	n	\bar{x}	$s_{\bar{x}}$	n
1996	1.74	0.24	21	1.41	0.21	22	1.57	0.16	43
1997	0.49	0.14	18	1.67	0.21	12	0.96	0.16	30
2000	0.57	0.18	9	0.27	0.09	7	0.44	0.11	16
Totals	1.05 ^a	0.15	48	1.29 ^a	0.15	41	1.16	0.11	89

^a Depth of rump fat did not differ significantly (2-tailed t -test with pooled variances) between moose residing year-round in the Tanana Flats versus moose that migrated seasonally into the Alaska Range foothills ($P = 0.267$).

Table 8 Average maximum rump fat depths among female moose ≥ 34 months old of various reproductive classes, March 1996, 1997, and 2000, central Unit 20A

Status of adult females	Maximum rump fat depths (cm)		
	\bar{x}	$s_{\bar{x}}$	n
Nonpregnant	0.25* ^a	0.12	13
Pregnant	1.32*	0.11	76
Nonparturient	0.68**	0.19	23
Observed parturient	1.38**	0.12	62
Single-producing	1.19***	0.13	50
Twin-producing	2.16***	0.27	12
Totals	1.16	0.11	89

^a Depth of rump fat differs significantly (2-tailed t -test with pooled variances) between categories of females at * ($P = 0.0002$), ** ($P = 0.004$), and *** ($P = 0.001$).

Table 9 Timing of parturition among radioed moose, 1996–2000, central Unit 20A

Year	Median calving date	Range of calving dates	Number of radiocollared cows giving birth (<i>n</i>)
1996	19 May	12–27 May (16 days)	35
1997	22 May	14 May–3 Jun (21 days)	29
1998	22 May	14–29 May (16 days)	30
1999	23 May	14 May–6 Jun (24 days)	33
2000	24 May	14 May–9 Jun (27 days)	48

Table 10 Annual survival rates of radioed moose, 1996–1997 through 1999–2000, central Unit 20A. Sample size is the maximum number of moose at risk.

Age of moose	Annual survival rates from mid-May through mid-May (%)							
	1996–1997		1997–1998		1998–1999		1999–2000	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Calves (0–12 months)	56	49 ^a	52	53 ^b	43 ^c	--	44 ^c	--
Yearlings (12–24 months)	--	--	87	41	67	47	83	42
2-year-olds (24–36 months)	--	--	--	--	100	24	96	28
3-year-olds (36–48 months)							100	24
Adults (≥ 36 months)	88	44	93	41	79	36	85	29

^a Maximum numbers of calves at risk at any time, 42 radio collars deployed in May 1996 and 29 in March 1997.

^b Maximum numbers of calves at risk at any time, 41 radio collars deployed in May 1997 and 29 in March 1998.

^c Calculated as number of calves/100 cows ≥ 28 months old × mean survival rate in 1996–1997 and 1997–1998 × mean number of calves/100 cows ≥ 28 months old in 1996 and 1997.

Table 11 Moose population modeling outputs using average values for moose composition, numbers, mortality and productivity of the various age classes in Unit 20A during 4 low to moderate snowfall years, 1996–1997 through 1999–2000. This modeled population is increasing at 0.4 % annually.

	Moose			Totals
	Adults ≥24 months old	Yearlings 12–24 months old	Calves 0–12 months old	
Precalving in Year 1	8230	1927	0	10,157
Calves produced	0	0	4489	4489
Killed by wolves	687	259	905	1851
Harvested	640	150	0	790
Killed by grizzly bears	127	49	557	733
Killed by black bears	0	65	626	691
Killed by other factors	147	32	209	388
Remaining at precalving in Year 2	*6629	1372	2192	10,193

APPENDIX A Relationships between blood-serum variables and depth of rump fat in Alaskan moose

KEECH MA, TR STEPHENSON, RT BOWYER, V VAN BALLEMBERGHE, AND JM VER HOEF. 1998. *Alces* 34:173–179.

Abstract: We studied the relationship between maximum depth of rump fat determined from ultrasound measurements and 22 blood values for Alaskan moose (*Alces alces gigas*) by sampling 38 pregnant, adult females. Moose were immobilized, and blood was drawn simultaneously with the determination of depth of rump fat during 1–4 March 1996. Multiple-regression models were used to detect relationships between blood-serum variables and depth of fat. Four of 22 blood-serum variables were removed to control for multicollinearity. Remaining variables were regressed against induction time ($\bar{x} = 6.1$ min, $SD = 4.4$ min). Glucose, sodium, and blood urea nitrogen were correlated with induction time ($R^2 = 0.27$, $P = 0.010$) and likely represented a response to handling; these blood values also were removed from the final regression model. Mallows' C_p statistic indicated the most appropriate regression model included only 2 variables. Creatinine ($\bar{x} = 2.08$ mg/dl, $SD = 0.26$ mg/dl) and aspartate aminotransferase (AST) ($\bar{x} = 79.10$ U/l, $SD = 13.61$ U/l) met all necessary assumptions and explained a portion of the variability observed in fat depth ($\bar{x} = 1.5$ cm, $SD = 1.0$ cm). Thus, our final model was: maximum depth of rump fat = $0.28 + 1.68$ (creatinine) -0.03 (AST). This model was significant ($P = 0.0002$) and accounted for 33.7% (R^2) of variability observed in fat depth. Partial regression coefficients for creatinine and AST were 0.222 ($P = 0.0025$) and 0.150 ($P = 0.006$), respectively, and indicated that creatinine was slightly more influential than AST in the model. These blood variables may provide insights into the predicted condition of moose and the response of moose to environmental conditions. A model using blood variables thought to be indicators of physical condition (protein, phosphorous, and calcium) did not explain significant variation in maximum depth of rump fat.

APPENDIX B Effects of birth weight on growth of young moose: Do low-weight neonates compensate?

KEECH MA, RD BOERTJE, RT BOWYER, AND BW DALE. 1999. *Alces* 35:51–57.

Abstract: We studied the relation between birth weight and 3 measurements of body size in 10 female Alaskan moose (*Alces alces gigas*) at 10 months of age in a population where density was high (1.3 moose/km²), compared with other areas of interior Alaska. Our study area was located in interior Alaska, USA, between the Tanana River and the Alaska Range, directly south of Fairbanks. We captured newborn (<5 days old) moose from helicopters, weighed them, and then affixed radiocollars during 14 May–3 June 1997. These same moose were immobilized with a dart-gun fired from a helicopter, weighed, and measured during 13–16 March 1998. We used regression analyses to investigate the relationships between weight at birth and weight, metatarsus length, and total body length for recaptured individuals at 10 months of age. Positive linear relationships existed between each measure of size at 10 months and weight at birth, and were highly significant ($P < 0.02$). Further, birth weight explained significant variability in each of those 3 measurements ($r^2 = 0.63, 0.64, 0.53$, respectively). Our results support the hypothesis that neonates with lower weights at birth in this population did not exhibit compensatory growth and remained among the smallest individuals in their cohort, at least during their first 10 months of life.

APPENDIX C Life-history consequences of maternal condition in Alaskan moose

KEECH MA, RT BOWYER, JM VER HOEF, RD BOERTJE, BW DALE, AND TR STEPHENSON. 2000. *Journal of Wildlife Management* 62:450–462.

Abstract: We studied life-history characteristics of Alaskan moose (*Alces alces gigas*) including the effects of maternal condition of adult females (>33 months old) on survival and physical condition of young during their first year-of-life. We also examined the relation between maternal condition and reproductive parameters of individual adult moose, and tested for effects of those parameters on timing and synchrony of parturition. We radiotracked adult females captured in both March 1996 and 1997 throughout the year with intensive monitoring occurring during spring and early summer. That procedure enabled us to capture the offspring of females we monitored and record other variables related to reproductive success. Females with greater rump fat thickness had higher rates of pregnancy, gave birth to more twins, and produced young with higher birth masses than did females with less rump fat. Time-to-death for individual young increased as birth mass increased and decreased as birth date and litter size increased; those birth variables, however, did not act upon time-to-death independently. Our results indicated maternal condition influenced subsequent variables associated with birth, which ultimately affected future survival of offspring. Further, timing of reproduction varied between the 2 years, with births occurring earlier but not more synchronously in 1996 than in 1997. Time of parturition occurred earlier for individual females with the thickest rump fat. That outcome indicated that timing of parturition was the result of environmental factors acting on females prior to giving birth rather than effects of attempting to avoid predation.